Territoriality and Homing Behavior in the Poison Dart Frog (*Dendrobates pumilio*)

MARGARET E. McVEY, ROBERT G. ZAHARY, DIANE PERRY AND JOHN MACDOUGAL

Male *Dendrobates pumilio* return home if displaced, suggesting that their vocal behaviors maintain territories. Many females are also site specific, perhaps because involved in parental care. Observations concerning mating behavior suggest that some *D. pumilio* are at times polygynous.

RECENT studies relating ecology to social behavior and mating systems in anuran amphibians reveal an impressive diversity of social systems (Emlen, 1976; Wells, 1977a, b). Careful characterization of such systems are not available for most species, however. In species with vocal, hyperdispersed males, behaviors have been labeled as individual avoidance or territoriality when data to distinguish between these two superficially similar systems are lacking (Wells, 1977a). This study of *Dendrobates pumilio* was therefore designed to 1) test for territoriality and 2) provide a preliminary description of some breeding behaviors.

*D. pumilio*, a "poison dart" frog (Meyers and Daly, 1976), is common in the Atlantic lowland tropical forests of Central America. It is diurnal and forages for small insects in leaf litter (Limerick, 1976). Both sexes are bright red with purple-blue legs and contain alkaloids in the skin (Albuquerque et al., 1971; Meyers and Daly, 1976). Males call from logs and tree bases. When such sites are evenly distributed on the forest floor, males appear to be hyperdispersed (Bunnell, 1973). Females lay eggs in moist leaf litter or under logs (Savage, 1968). Adults carry tadpoles from the ground to water-filled bromeliads (Starrett, 1960). Both males and females are reported to carry tadpoles (Kitasako, 1967; Silverstone, 1975; Wells, 1977b).

Individual males remain in the same spot for many days and occasionally attack approaching intruders (Bunnell, 1973). Aggressive behaviors can be provoked by playing male calls through a speaker 1–2 m from a calling male (Bunnell, 1973), but such provocation does not distinguish between territoriality (defense of a site) and individual spacing with slow rates of movement. If a male is territorial, he defends a specific site on which he is dominant to conspecifics (Brown, 1963). If held for breeding purposes, this site could contain reproductive resources, a nest site and a buffer zone for spacing, or be a lek position. Because sites differ in quality, a male's territory should influence female choice. Most males should therefore be strongly attached to their territory. If a male is simply avoiding proximity to other males, however, he should not be more attached to one calling spot than to another.

In this paper, we describe the spatial dispersion of marked males and females in relation to physical features of the environment and report results of homing experiments with both males and females. We also examine the possibility that simultaneous polygyny occurs in this species.

**METHODS**

We conducted this study from 29 July to 3 August 1977, in the arboretum of the Organization for Tropical Studies field station at Finca La Selva, near Puerto Viejo de Sarapiqui, Heredia Province, Costa Rica. The arboretum consisted of widely spaced trees (10–15 m between trunks) with some small saplings interspersed. There was little brush or understory. Ground cover consisted of mixed grasses, ferns, leaf litter and occasional logs and stumps. The arboretum has been maintained this way since 1968. We marked and mapped two rectangular study
areas, each approximately 1,000 m² (20 x 50 m) in area. The plot selected as the experimental plot (plot E) had its long axis adjacent to a thick wood on the western edge of the arboretum, and the control plot (plot C) was parallel to it, approximately 20 m south, 4 m lower in elevation, and 20 m from the nearest forest edge.

We censused plots daily, between 0600 and 1100 h, by moving slowly through the plot, four abreast, and searching all reachable substrates for 1.5 h (6 person h). Each frog captured was toe clipped, sexed and released at the capture site which we staked and later mapped. Male D. pumilio bear a buff colored patch on the ventral surface of the throat (the gular sac) which females lack (N. Scott, pers. comm.). Some frogs bore blue streaks ventrally which obscured their throat color and we called these of "indeterminant" sex. No other large frogs (20-23 mm snout to vent) were of indeterminant sex. Three smaller frogs were not included in the study. For recaptures, the position was located by compass direction and distance from the stake marking the original capture position. All trees in each plot were censused for bromeliads.

A displacement experiment to determine homing tendencies was performed in plot E on the third day. Each censused frog was placed in a plastic bag at its capture site and shaded with leaf litter to minimize thermal stress. At the completion of the 1.5 h census, the bagged frogs were displaced to release sites. Males were divided into two groups, while female frogs, being more numerous, were divided into four groups (Table 1). Release sites were chosen such that all four cardinal compass directions were represented in each displacement group, all 16 compass points were represented overall, no frogs were displaced from the plot, and the density of frogs at any site remained relatively unchanged. After all frogs had been displaced, we opened the bags and released the occupants. To control for the effects of bagging, all individuals captured in plot C during the census of the same day were bagged (but not displaced), and released after 1.5 h.

From 26 to 31 August 1977, the first author recensused the plots daily from 0600 to 1200 h. In this report ± after a mean value signifies 1 sd.

### RESULTS

**Population density.**—The density of both sexes within the plots was determined from population estimates for each plot derived using Jolly's modification of the Lincoln Index (Jolly, 1965). Successive calculations of population size for each day will approach an asymptote representing the true population size if the population is closed (no immigration, emigration, births or deaths).

Density in plot C, located nearer the middle of the arboretum, was less than half that of plot E, which bordered rainforest edge (Fig. 1). Assuming no emigration occurred, our calculations indicate that 10-15 males and 36-43 females resided in plot C (1,050 m²), yielding a density of approximately 1.3 males and 3.8 females per 100 m². Between 26 and 33 males (of which 25 were marked) resided in plot E (1,160 m²), a density of 2.7 per 100 m². Six frogs of indeterminate sex were captured in plot C, and 11 in plot E. The uniformity of the population estimates after day three suggest low levels of influx and efflux of males. The estimate of females in plot E, on the other hand, rose markedly on day four, suggesting a large influx of unmarked females on that day. Five females would account for such a change, and four new females were found in a previously unoccupied location at the wood's edge. In plot E, the female population consisted of between 107 and 137 individuals (81 marked). This density of about 10.6 females per 100 m² is 2.8 times the estimate for plot C. The total population density of plot E was 2.5 times that of plot C.

### Table 1. Translocation Experiments. Numbers of individuals moved and recaptured, by sex and by distance, in experiments.

<table>
<thead>
<tr>
<th>Meters displaced</th>
<th>3</th>
<th>6</th>
<th>12</th>
<th>20</th>
<th>Total</th>
</tr>
</thead>
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<tr>
<td><strong>Females:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Moved</td>
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<td>6</td>
<td>6</td>
<td>6</td>
<td>23</td>
</tr>
<tr>
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<td>6</td>
<td>5</td>
<td>5</td>
<td>20</td>
</tr>
<tr>
<td><strong>Males:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Moved</td>
<td>0</td>
<td>4</td>
<td>5</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td>Recaptured</td>
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<td>3</td>
<td>5</td>
<td>0</td>
<td>8</td>
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<tr>
<td><strong>Totals:</strong></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Moved</td>
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<tr>
<td>Recaptured</td>
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<td>9</td>
<td>10</td>
<td>5</td>
<td>28</td>
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</table>

COPEIA, 1981, NO. 1
Sex ratio.—The female/male ratio for both plots consistently exceeded one. Two different methods of estimating sex ratio yielded slightly different results. The mean F/M ratio from the last four Lincoln Index estimates, 3.5 and 3.6 for plots C and E respectively, were higher than the sex ratios for all identified frogs, 2.8 and 2.7, C and E. The difference between these calculations could result from a higher probability of recapture for males and/or a higher emigration rate for females.

Probability of recapture.—The probability of recapture (calculated as the number of recaptures divided by the number of censuses after the frog was marked) represents a more direct assessment of sampling bias by sex (Table 2). Frogs were less likely to be recaptured on a daily basis in plot E than in plot C (Table 2). This could result from greater movements between plot E and the forest than between plot C and the surrounding arboretum, or a greater number of hiding places in plot E.

Males were 1.9 and 1.5 times more likely to be recaptured than females in plots E and C respectively, a significant difference for the combined plots ($\chi^2 = 6.69; 1 \text{ df}; P < 0.02$). However, despite sampling bias in favor of males, the population in the arboretum was over 70% female.

Male dispersion patterns.—Calling males that were recaptured on several days in a circumscribed area were no closer to their nearest calling neighbor than 2.5 m. In plot E, the mean distance between nearest neighboring males was $4.8 \pm 2.0$ m ($N = 18$). These calculations incorporate only calling posts simultaneously maintained over two or more days. Such spacing could result from males defending territories of at least 2.5 m diameter or simply avoiding other males more than 2.5 m away. Because males generally called from tree bases or fallen logs, the distribution of such sites determined the larger inter-male distances (Fig. 2). A modified form of the Clark/Evans dispersion index (Pielou, 1969) was calculated as 0.86 for the males alone (derived from an expansion of Fig. 2, which represents about 80% of the total male population). For this statistic, a value of 1 indicates a random distribution, a value of less than 1 indicates an aggregated distribution, and a value greater than 1 indicates hyperdispersion.

Residents of four of 30 calling sites changed during six days. On day two, three males were captured near each other, but later spaced

<table>
<thead>
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<th>Table 2. Recapture Data by Sex and by Plot.</th>
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<tbody>
<tr>
<td>Parameter</td>
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<td>Number of individuals</td>
</tr>
<tr>
<td>Possible number of recaptures</td>
</tr>
<tr>
<td>Actual number of recaptures</td>
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<tr>
<td>Probability of recapture</td>
</tr>
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</table>
themselves and called from new locations. In another area, a new male appeared next to an "established" male on day four, but was never seen again. On still another log, we captured four different males, but no more than two were present on any one day, and only one was calling at the time of capture. Thus, although most calling males occupied only one area during the study, some seemed to be contesting sites and some moved between sites.

Female dispersion patterns.—Females occurred singly or in groups of two to five. Groups were of two types. In a stable group, the same females were at the base of a tree for three to six days, although not all females were found each day. Stable groups always occurred around a tree containing bromeliads. A temporary group was one in which several females appeared together on only one day. While some stable females were not associated with a male, all temporary groups were. Females from two of the temporary groups extruded 1–3 eggs when captured. For females alone, the modified Clark/Evans dispersion index was 0.35 (from Fig. 2, which represents 66% of the total female population). Thus, females showed a more clumped distribution than did males.

Movement patterns.—To determine the proportion of stationary and mobile males and females, we calculated an index of mobility (MI) for each frog as follows:

\[
MI = \frac{D}{N} \text{ where:}
\]

\[
D = \text{diameter (m) of a circle inscribing the plot of all daily movements, and}
\]

\[
N = \text{number of days from first to last capture.}
\]

Only frogs captured two or more times were used. Frequency distributions of MI values for each plot and sex are shown in Fig. 3. Individuals marked in one plot were never recovered in the other. To the extent that failure to recapture an individual for several days resulted from the probability distribution of multiple recaptures (which can be derived from Table 2) rather than movement from the plot, results are biased toward lower MI values for males.

Of 21 males, 71% had an MI of one or less, and of 60 females, 53% had an MI of one or less. Because of the bias mentioned above, it appears that the mobilities of males and females are indistinguishable. MI of less than one corresponded to movements of 3 m or less; eight males and 24 females were recaptured within two decimeters of the same place day after day. Males with an MI less than one sat at fallen logs or tree bases. Seventy % of the females in this group were at the bases of trees or logs with bromeliads, only half of which had resident males.
Displacement studies.—On day three, we displaced frogs to test for homing. Males were transported beyond the potential territory of their nearest neighbor (Table 1). Fourteen males captured two or more days in this plot were not captured on this day, so some displacements could have placed the moved individual into an occupied territory. Our census maps revealed later that five males were moved into areas from which a resident also had been displaced, and we had placed another male in a portion of these five males’ original home area. Due to the greater number of individuals, females were displaced over greater distances than males (Table 1).

We used two measures of homing ability. 1) Our first measure was the distance from the home site (location on day three, prior to displacement) to place of first recapture. If, after displacement, a frog simply moved randomly over distances typical of control frogs, one would expect the distance between home and the point of recapture to approximate the translocation distance (line A, Fig. 4a, c). Of the 12 female frogs displaced 12 or 20 m, ten were found within 6 m of home (2 not recaptured). Of the nine males displaced, six were found within 2 m of home.

2) Our second measure was the direction of movement. Following displacement, the tendency for individuals to travel in the homeward direction was statistically significant for females and nearly so for males (P < 0.001, P < 0.10 respectively, Fig. 4). If one adds the animals not recaptured, however, as though they traveled 90° and 180° away from home (open circles, Fig. 4), the 0.10 level of significance is lost for males and P < 0.01 for females. Sixty-six % (6) of the males traveled within 15° of the home direction, a proportion similar to the proportion of males that restricted movements to within a 3 m diameter (MI < 1). All five of the males transported into vacated territories homed. Fifty-eight % of the females traveled within 22° of the home direction, again a proportion similar to those restricting movements to within a 3 m (MI < 1) in the remaining population. Undisturbed animals in both plots were as likely to travel long distances as animals which had been placed in bags and released with no displacement.

Duration of residency.—During the week of 26 to 31 August, about one month after the first week of censusing, the arboretum seemed drier and frogs were more difficult to find. Because only one person searched for five hours, meaningful comparisons with the previous month’s data are impossible. Of the 43 males marked earlier, 18 were recaptured, but only 11 unmarked males were found. Of the recaptured males, 56% were within 2.5 m of their previous location (Fig. 5). Thus at least 23% (10/43) of the males had probably maintained the same territory for a month. Thirty-three % were within 5 m of their previous month’s location, but whether 2–5 m represents the same territory or not we cannot determine. Of the 118 females marked earlier, 40 were recaptured but only 18 unmarked individuals found; 45% were within 2 m, 58% within 3 m of the previous month’s most frequent location.

Behavioral observations.—On the morning of 30 July, MacDougal observed mating between a male and a female in plot E. The female approached the male, which was at the base of a log, and passed him to walk under the log, at which point the male followed, joining the female on a convex leaf. Interactions between the two were similar to those Crump (1972) reported for D. granuliferus, except that the sequence was interrupted when the male left the female, walked one m away, called, and was approached by another frog. The male then returned to the female with the third frog following. After mating vent to vent, the female deposited three eggs on the leaf. These events lasted from 0730 to 0830 h. The male then returned to the edge of the log and called; the female moved away with the third frog, later sexed as a male, following her. The original
male then returned to the eggs and sat on them. We did not disturb him again. When we checked the leaf 24 h later, we found no frog in attendance, but 11 eggs on the leaf. After 48 h it was clear that three groups of eggs (three, four and four) of different sizes were present, although the groups were close to each other.

On 30 August, McVey observed a female in the forest near the station carrying a single tadpole on its back into a water-filled bromeliad on the ground. After it released the tadpole into the water, the frog was captured and sexed. After release, the frog hopped under a nearby log where she remained for 2 h. Possibly because McVey disturbed her, the female disappeared into the forest.

**DISCUSSION AND CONCLUSIONS**

Our study supports claims that male *D. pumilio* are territorial. Not only did many males (23%) remain in a restricted area over one month's time, but most (66%) returned home even when displaced over distances up to 12 m (approximately 5 times the territory diameter). These results are not due simply to displacement of individuals to unsuitable habitats, for in at least five cases individuals were displaced into territories made available by the simultaneous displacement of the resident.

Site fidelity might result if site familiarity contributed to predator avoidance or food gathering efficiency, but neither of these pos-
sibilities appears appropriate for *D. pumilio*. The frogs are aposematic and feed on small leaf litter insects (Limerick, 1976) which are not concentrated at bases of trees. Thus, the strikingly similar patterns of movement for males and females probably reflect other causes.

We believe that male *D. pumilio* are defending territories which include both a calling perch and oviposition sites. All calling locations included both items, but not all included bromeliads or leaf litter. The minimal territory diameter of 2.5 m suggested by both Bunnell’s (1973) and our work might ensure a minimal interclutch distance important to avoid predation.

We hypothesize that females homed because they were monitoring tadpoles or guarding eggs. We observed a female *D. pumilio* carrying a tadpole. Fifty % of the females in our displacement experiment homed to within 3 m of their original capture site, and 37% of all females remained for days at the bases of trees or logs with bromeliads. Because many of these sites did not contain males, leaf litter or refugia, but all contained bromeliads, tadpole monitoring by females is suggested.

The unusual sex ratio of 3.5 F/M in the arboretum is perhaps the result of tadpole monitoring. Because male and female mobility measures were so similar, we believe the Lincoln Index sex ratio estimates to be good ones. The sex ratio of all individually identified frogs (2.7 F/M) is not a good estimator because males were more likely to be captured than females. Bunnell (1973) found a F/M ratio of 0.8 in rainforest at La Selva where the denser vegetation and reduced light penetration allow fewer bromeliads to grow within 10 m of the ground. If males are defending oviposition sites and females predominantly tending tadpoles in bromeliads, one would expect a lower F/M ratio in the rainforest than in the arboretum, as was observed.

We suggest that some *D. pumilio* are simultaneously polygynous at some times. We observed one female to lay three eggs for a male and leave; yet 24 h later eleven eggs were present on the same leaf. Crump’s (1972) observation that the range in clutch size for four clutches in the closely related *D. granuliferus* was three to four per female suggests that three different *D. pumilio* laid these eggs. During the two week study we also observed two temporary aggregations of three and four females with a single male in which two females in each group extruded eggs upon capture. This also suggests that a male can attract several females to an oviposition site and receive a compound clutch. As these observations indicate, this species presents intriguing possibilities for studies of the sexes’ roles in parental care.

**Acknowledgments**

This research is partially comprised of work done during field course 77.4 of the Organization for Tropical Studies. The work was supported in part by NSF Research Initiation and Support Grant # SER76-17508 to McVey. Authors Zahary and Perry thank the Graduate School and the Department of Biology at the University of Southern California, and the Allan Hancock Foundation for grants funding their travel to Costa Rica and OTS expenses. We are indebted to K. Wells, J. Savage, E. Stiles, V. Vance, P. Starrett, M. Hartman, G. Rodda and M. Ryan for their careful and critical review of this manuscript, both in its current form and earlier versions.

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